"Southern" Is An Ecological Rather Than Geographical Trait

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Steelhead habitats show a very general change in characteristics from north to south in California, and populations were lumped into separate evolutionarily significant units (ESUs) based partly upon these differences. Additional support for ESUs came from neutral genetic markers that showed changes north to south that reflect decreasing amounts of gene flow with distance between populations. Some have treated these general north south patterns as a rigid guide to population ecological traits and management concerns and actions. For example, the suggestion is often made that "southern" steelhead can tolerate higher water temperatures and more frequent drought conditions. This approach ignores substantial ecological variation in habitats within geographical regions and also the ecological flexibility of steelhead throughout their California range.

"Southern" as an ecological trait of habitats and steelhead populations includes various degrees of the following: 1) the importance of year to year variation in streamflow as a factor affecting successful adult access to spawning areas in winter and smolt emigration in spring; 2) the importance of higher temperatures as a factor regulating survival and microhabitat use of juvenile steelhead and their interactions with other fish species; and 3) the importance of large-scale habitat alterations from diversions and urbanization upon migration difficulty and rearing habitat suitability. Certainly, many steelhead habitats at the southern portion of the species' range have these traits. However, some do not, and many "northern" populations are faced with these challenges.

Topographical features of the coastal and inland portions of watersheds strongly affect the habitat conditions in which steelhead live. Access to and from the ocean is relatively easy in most years where the streams are small and occur in rugged coastal terrain. The streams of the Big Sur coast provide easy access, relatively cool summer water temperatures, and rural conditions. Ecologically, these are "northern" streams, although they occur in the south-central coast ESU. Further north the Salinas and Pajaro River watersheds extend inland across broad coastal valleys, with a majority of the watershed on the eastern (rain-shadowed) side of the coast range. Access to and from the ocean was probably restricted during drought, even before agricultural and urban development dammed the tributaries and modified much of the lowland portions of the watershed. Much of their stream habitat is warm, and warm-water native fishes, including Sacramento pikeminnow, California roach and hitch share low and mid-gradient habitat with juvenile steelhead. Similarly, the Russian River at the northern boundary of the central coast ESU, has extensive warm, inland habitat. Even much of the main stem of the Eel River is warm-water habitat. The tributary streams to South San Francisco Bay are within the central coast ESU, but as inland, urbanized habitats they are warm and highly modified. Headwaters support resident rainbow trout and steelhead, but adult and smolt migrations are restricted or blocked on many streams in most years. Less than 10-30 miles to the west most small coastal streams in San Mateo and Santa Cruz counties are relatively cool, rural, and usually provide reliable access to and from the ocean.

Habitats with higher water temperatures are found throughout the range of California steelhead, and in some cases provide important steelhead rearing. The upper lethal temperature for steelhead in laboratory studies (28 to 31 degrees C) is far above the typical habitats where steelhead are *usually* found. Below this physiological limit, temperature exerts its influence by raising metabolic (food and oxygen) demands and by affecting swimming and competitive performance. Sublethal temperatures are often a food, rather than a water quality issue. Many coastal lagoons from northern through southern California can have high water temperatures (afternoon temperatures of 20-24 degrees C) during some or much of the summer, but rear abundant, fast growing ("southern") steelhead. If the lagoon is well-mixed (by wind or conversion to freshwater), and amphipods and shrimp are abundant as potential steelhead food, young-of-year steelhead may reach 150-200 mm (6-8 inches) long by the end of their first summer and smolt as yearlings in winter or spring. Cooler, but food-limited, upstream habitats provide more typical ("northern") steelhead conditions, but most steelhead there require 2 years to reach smolt-size. Young-of-year fish may be abundant upstream, but the lagoon may provide a substantial portion of the watershed smolts. *If food is abundant*, the warmer water actually allows faster growth by speeding digestion. Occasionally, on-channel seasonal dams can provide similar fast-growth habitat, if food is abundant *and* if competition from warm-water fishes is not a problem.

Where summer streamflows are naturally high (the gorge of the San Lorenzo River) steelhead can often find sufficient food (as drifting insects) in fast-water habitat to meet the metabolic costs of higher water temperatures. Rapid growth and smolting as yearlings is typical in such habitats, and the extent and production of this habitat expands in wetter years. In many developed watersheds (Russian and Carmel rivers and Alameda, Stevens, Uvas and Nacimiento creeks) water temperatures below dams are relatively high during much of the summer, but summer streamflows have been substantially increased to utilize the channel to convey or percolate water. In some of these streams the fast-water habitat provided by the enhanced streamflow provides the drifting food necessary for steelhead to survive (and often grow quickly) despite the metabolic costs of the higher water temperatures. Total numbers of fish may seem small compared to the abundant slow-growing fish of trickling, cool "natural" habitats, but annual smolt production may be relatively high.

Because of the wide variation in habitat types and potential steelhead responses, "it depends" is an appropriate answer to questions such as, "what temperatures do south (or north or central) coast steelhead require." Sampling the habitats to determine fish numbers and growth rates is likely to turn up some surprises, making for some interesting studies, and hopefully, a flexible regulatory response.